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Feeding activities and assimilation efficiencies of *Lumbricus rubellus* (Lumbricidae) on a plant-only diet

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With 3 figures

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1. Introduction

Many soil-inhabiting invertebrates not only feed on organic material but also show that inorganic soil particles are most important components in the diet. The same may be true for the burrowing earthworm *Allolobophora rosea* (see Bolton & Phillipson 1976). This species belongs to the mineral-organic horizon dwelling lumbricids (= endogée, Bouché 1972) which eat their way through the soil, selecting the more organic fractions.

Our investigations on earthworms have shown not only mineral-organic horizon dwellers but also epi-endogenic, pigmented litter dwellers such as *Lumbricus rubellus* produce faeces with a considerable portion of inorganic soil material, when living in pastures on prealpine and alpine woods as described by Martinucci & Sala (1979). Evidence from alpine larch stands also suggest that *L. rubellus* may live in litter layers (Bochter 1984) where no inorganic material is available.

The present study investigates feeding and egestion activities of *Lumbricus rubellus* when the only available food is plant material. For feeding treatments we used larch litter and alder leaves. Assimilation efficiencies for these different food resources have been calculated.

2. Materials and methods

Alder leaves and one-year-old larch litter were collected in autumn 1982 and stored air-dried (60% R. H.) at 15 °C.

At monthly intervals from December to May *L. rubellus* Hoffmeister, 1843 were collected in the field by digging and hand-sorting, transported to the laboratory and placed in two containers (20 cm × 20 cm × 8.5 cm) filled with wetted soil and leaves. One of these containers was kept at 15 °C for 10—14 days in order to acclimatize the worms to laboratory conditions. The second one was kept at 5 °C.

For feeding experiments small boxes (7 cm × 6 cm × 3.5 cm) were prepared with a 0.5 cm thick layer of synthetic sponge wrapped in fine gauze in the bottom. The watered sponge provided high moisture for several days. Only one adult specimen of *L. rubellus* was placed in each box. After that, either air dried alder leaves or larch litter were added. For each series we examined 40 parallel samples.

Undefined mineral particles in the gut of the worms could falsify our analysis on feed samples from former feeding. Therefore the worms were removed after 5 days from feeding boxes and placed into new ones adding the same kind of food. Mass of food (air dried) and mass of the worms (fresh mass) were noted. After 14 days the worms were removed and weighed. Food and faeces were collected carefully, air dried at 60% R. H., weighed and stored deep-frozen at —22 °C for calorimetric analysis.

A parallel series of litter samples, without the presence of earthworms, was additionally examined to measure losses which could occur as a consequence of microbial activity or loss of water.

Energy determinations were made in a modified microbomb calorimeter (Phillipson 1964). Energy values for all materials were calculated on an ashfree dry mass basis. Samples were ashed in a muffle furnace at 450 °C.

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3. Results

3.1. Consumption

Different indices of consumption have been proposed. We calculated the dry mass-fresh mass consumption rate (C.I.) from the dry mass of the food (C) eaten per day (T) and the fresh mass of the earthworm (= A):

$$\mathrm{C.I.} = \frac{\mathrm{C}}{\mathrm{T\,A}} \qquad \text{(Waldbauer 1968)}$$

Fig. 1 shows the consumption for *L. rubellus* while feeding on alder leaves at 15 °C. Table 1 summarizes the consumption rates for the alternative food sources at 5 and 15 °C and also indicates the egestion within the four series. Mean consumption rates (C.I.) measured in different months are given in Fig. 2.

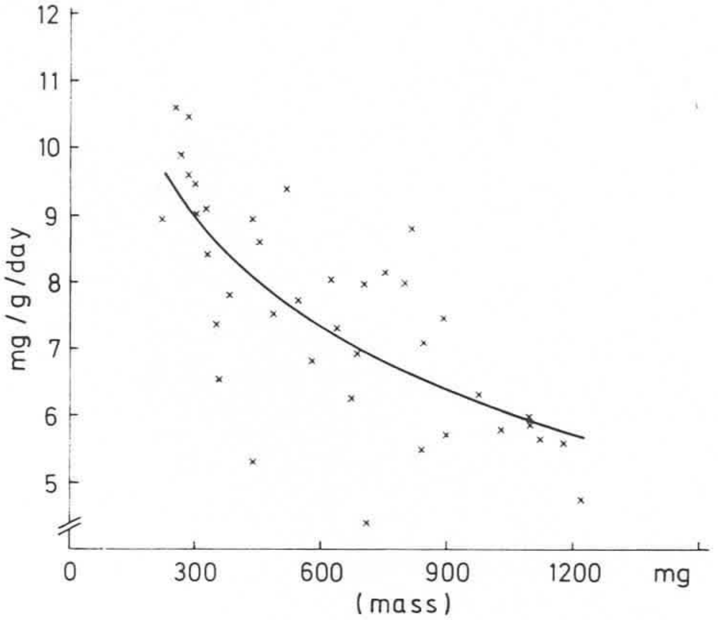

Fig. 1. Consumption rate of *Lumbricus rubellus* of different sizes when feeding on alder leaves at 15 °C.

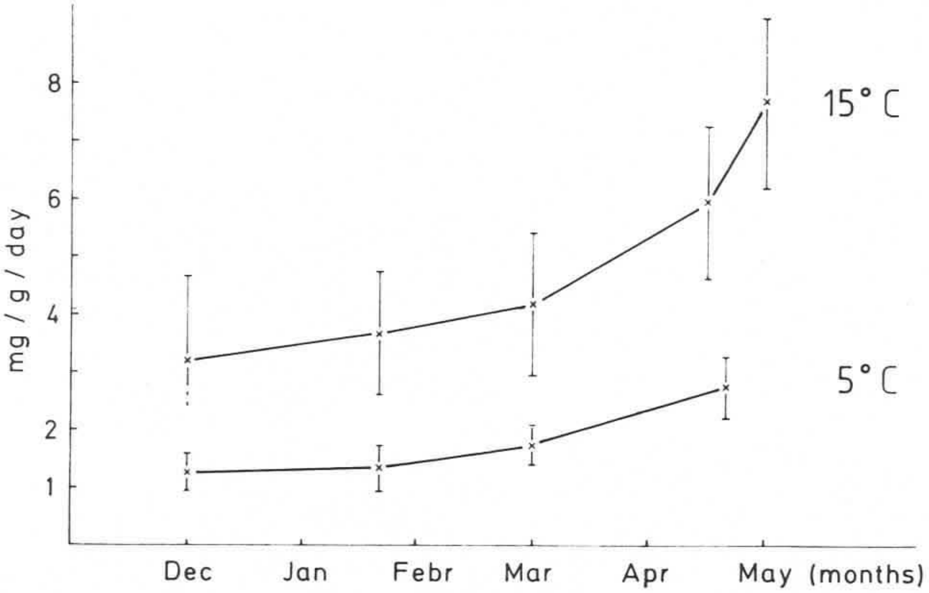

Fig. 2. Influence of annual periodicity on consumption rate of *Lumbricus rubellus* when feeding on alder leaves at 15 °C. The quality of food during the period of investigation was standard ($\bar{x} \pm$ S.D. for 40 parallel samples each).

Table 1. Consumption and egestion rates of *Lumbricus rubellus* feeding on alder leaves and larch litter at different temperatures (mg g^{-1} d^{-1}) (±SD)

	°C	alder	larch
consumption:	5	2.72 ± 0.55	0.64 ± 0.47
	15	7.59 ± 1.56	3.08 ± 1.27
egestion:	5	0.62 ± 0.57	0.43 ± 0.24
	15	2.55 ± 0.86	2.30 ± 0.91

The consumption rate is not the same for small immatures and adult specimens. A direct relationship occurs, however, if consumption is quoted against the metabolism of the worm. As a rough estimate for basal metabolism the surface area is calculated as $\sqrt[3]{A^2}$ (GERE 1956). If we use this factor in the above-mentioned formula we get

$$CQ = \frac{C}{T\sqrt[3]{A^2}}$$

the consumption rate quotient CQ which is nearly constant for specimens of all sizes of earthworms. With alder as food this gives a value of $\bar{x} = 2.18 \pm 0.34$ (%) at 5 °C increasing by a factor of 2.8 to $\bar{x} = 6.11 \pm 0.96$ (%) at 15 °C. When larch litter was eaten, the consumption quotient was increased by a factor of 4.8 when values at 5 and 15 °C were compared.

3.2. Digestibility

The approximate digestibility (A.D.) illustrates the percentage relation of the assimilated food to the consumed food, and is calculated as (F = mass of faeces):

$$A.D. = \frac{C - F}{C} \times 100\ (\%) \qquad \text{(WALDBAUER 1968)}$$

Among leaf-feeding or litter feeding species digestibility varies widely with the species of food plant. In our results we found a range from 68.8 ± 11.1% at 15 °C to 76.4 ± 10.6% at 5 °C for alder leaves and a range from 21.3 ± 10.8% at 5 °C to 24.3 ± 13.9% at 15 °C for larch litter.

3.3. Utilization of energy

Energy levels of food and faeces were determined for all trials. Additionally the ash content of dry materials and its calorific value was ascertained. From this, ash-free calorific values of materials for all trials were calculated (Table 2). Percent ash was significantly higher in faeces than in food. Ash-free calorific values of food and faeces did not differ significantly within or between trials.

In order to analyse utilization of energy, average ash-free calorific values of daily food input and production of faecal pellets were measured. Food input was always highest (157.5 ± 32.5 J g^{-1} d^{-1}) when animals were fed on alder leaves at 15 °C. At 15 °C animals increased their consumption to 58.3 ± 24.2 J g^{-1} d^{-1}.

Table 2. Calorific values (E_{tot}), percent of ash content and ash-free calorific values ($E_{afr.}$) of feeding trials (±S.D.)

food				faeces	
				15 °C	5 °C
alder	E_{tot}	J/mg	19.658 ± 0.862	15.479 ± 0.675	14.121 ± 0.642
	ash	%	5.51	18.55	28.84
	$E_{afr.}$	J/mg	20.808 ± 0.925	19.017 ± 0.837	19.783 ± 0.842
larch	E_{tot}	J/mg	18.437 ± 0.537	15.367 ± 0.896	15.856 ± 0.921
	ash	%	6.96	14.85	18.70
	$E_{afr.}$	J/mg	19.817 ± 0.921	18.046 ± 1.054	19.517 ± 1.133

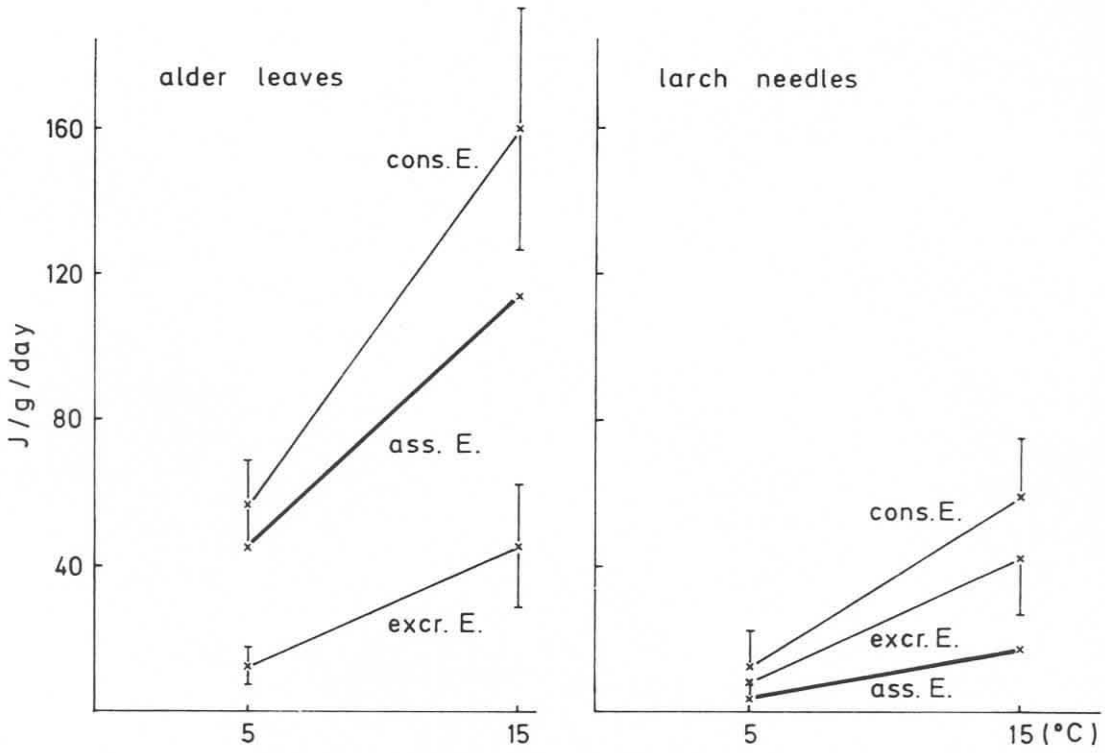

Fig. 3. Energy values of consumed material (larch litter and alder leaves) eaten by *L. rubellus*, of the faeces and of the assimilated food when reared at 5 and 15 °C. The values are based on ash-free data and take into consideration microbial activity and/or decrease by leaching ($\bar{x} \pm$ S.D. for 40 parallel samples each).

Production of faecal pellets varied with temperatures as did food consumption. However, in contrast to food consumption defaecation was not significantly different when the animals were fed on alder leaves or larch litter (Fig. 3). The utilisation of energy (coefficient of metabolizable energy (C.M.E.), WALDBAUER (1968) was measured by the ratio of assimilation to consumption. It appears that the utilisation of energy was relatively high when animals were fed on alder leaves at 15 °C: 71.6 ± 11.5%, and at 5 °C: 78.4 ± 10.9% and relatively low when animals were fed on larch litter at 15 °C: 28.7 ± 16.4% and 5 °C: 33.7 ± 17.1%.

Assimilation efficiencies measured gravimetrically or by calorimetry did not differ from each other. Calorific values of food and faeces were nearly the same.

4. Discussion

In our laboratory feeding experiments 50% of the specimens were provided with larch litter because this could be one of the most important food resources in some alpine sites where several individuals of *Lumbricus rubellus* were found. However, earthworms in the laboratory at 15 °C consumed only 3.08 ± 1.27 mg g^{-1} d^{-1}. At 5 °C consumption rate was even much lower.

The remaining specimens were fed with alder leaves because this diet is well known for its good digestibility and quality for most soil dwelling invertebrates. Feeding on this food source consumption rate at 15 °C was as high as 7.59 ± 1.56 mg g^{-1} d^{-1}; this is equal to 157.5 ± 32.5 J g^{-1} d^{-1}.

These data were based on ash-free values and also took into consideration microbial activity and/or decrease in mass by washing out (*cf.* BOCOCK *et al.* 1960). When placed into the feeding boxes for two weeks at 15 °C losses in dry mass for larch litter were only about 1.9% and for alder leaves 19.4 ± 2.0%. During the same time period decrease in mass for *Quercus* and *Fagus* leaves is 4—5% whilst leaves from *Sambucus nigra* lose as much as 57% of their mass (DÓSZA-FARKAS 1976).

Previous records of consumption rates of earthworms generally exceed these results. ZICSI (1975) calculated the consumption rate for two *Lumbricus* species at 20—25.5 mg g^{-1} d^{-1} and SATCHELL (1967), who compiled data from several authors, gave a mean consumption rate of 27 mg g^{-1} d^{-1}. But in all those experiments earthworms had the opportunity to feed on inorganic material. If they do so gut turnover may increase, thus decreasing the approximate digestibility of food. BOLTON & PHILLIPSON (1976) calculated the gut turnover time for *Allolobophora rosea* — a species which is highly adapted to the rapid turnover of large quantities of soil — to be in the range 1—2.5 hours. This is a much faster time than has been estimated for other lumbricids (BARLEY 1959). For *Lumbricus rubellus* gut turnover time was calculated to approximate 36—48 h when feeding on alder leaves or larch litter.

Consumption rates measured by POBOZSNY (1975) are similar to our results. *Lumbricus polyphemus* consumes *Carpinus betulus* leaves at the rate of 4.3—5.6 mg g^{-1} d^{-1}, whereas *Dendrobaena platyura* ssp. *montana* eats 1.9—3.4 mg g^{-1} d^{-1} at 10 °C. Feeding experiments with *Lumbricus rubellus* which were carried out by FRANZ & LEITENBERGER (1948) yielded data which lie within the range of consumption rates submitted here, when corrected for ash-free values and microbial activity. These relatively low consumption rates found by POBOZSNY (1975) and FRANZ & LEITENBERGER (1948) were obtained even though the species tested had the opportunity to feed on sand or clay particles.

Egestion rates of *Lumbricus rubellus* at 15 °C were independent of food source. At 5 °C a slightly lower value in egestion of larch needles was observed. Because *L. rubellus* did not feed on soil particles, in these experiments even egestion values as low as 2.35 mg g^{-1} d^{-1} were much lower than those reported in the literature. POBOZSNY (1975) calculated egestion rates in the range 69—204 mg g^{-1} d^{-1}; PIEARCE (1976) documented 48.8 mg g^{-1} d^{-1} for *Lumbricus rubellus* and the well investigated species, *Allolobophora rosea*, by BOLTON & PHILLIPSON (1976) even egested 1,000—5,000 mg g^{-1} d^{-1}. These values are 5—12 times higher than the 200—420 mg g^{-1} d^{-1} reported for *Allolobophora caliginosa* by BARLEY (1959). Data for both burrowing *Allolobophora* species are the highest recorded values for any earthworm.

The effects of temperature on egestion rates have been noted previously. For *Allolobophora rosea* (see BOLTON & PHILLIPSON 1976) the range of rate of increase in egestion within the temperature range 4.4—14.8 °C was 1.6—2.5. This can be compared to a much larger Q_{10} of 12.9 which MITCHELL (1979) found in the sludge worm *Eisenia fetida* over the temperature range 5—15 °C. The results for *Lumbricus rubellus* lie in between. The changing rates of egestion with temperature were somewhat but not significantly higher than the ingestion rates. When egesting alder leaves a Q_{10} of 3.8 was calculated, whereas the temperature-dependent egestion rate for larch litter was about $Q_{10} = 5.3$. Feeding activity of earthworms is influenced by temperature. Over the temperature range 5—15 °C feeding on alder leaves a Q_{10} of 2.8 was calculated, but when larch litter were used as food a Q_{10} of 4.8 was obtained.

Consumption rates are also influenced by annual periodicity. The first clue to our understanding of this process was provided by POBOZSNY (1975) who fed earthworms at constant 10 °C with dried *Carpinus betulus* leaves over a period of $2^1/_2$ years. Our studies at constant temperatures added further evidence. At 5 and 15 °C we also found a significant increase of consumption (Fig. 2), although the quality of food during the period of investigation was almost the same. In all trials microbial activity was taken into account.

From this one can assume that not only do species which apparently aestivate or hibernate (EDWARDS & LOFTY 1977) show a metabolic decrease during diapause, but also surface dwellers such as *Lumbricus rubellus* show a response which is not directly correlated to temperature. Decrease in consumption rate during winter months occurs although cocoon production does not totally cease. The annual cycle of reproduction in *Lumbricus rubellus*, therefore may be similar to *Allolobophora chlorotica* and *A. caliginosa* (GERARD 1967).

There are only few comparable data on assimilation efficiencies for earthworms. Very low values were calculated for *Allolobophora rosea* by BOLTON & PHILLIPSON (1976). These may reflect the rapid turnover of soil shown by this species. When calculated for energy values, assimilation energy in *A. rosea* was about 1%. When dry masses of organic material were used instead of energy content the approximate digestibility did not exceed 2.5%.

Assimilation efficiencies of *Lumbricus rubellus* obtained from energy values were of the order of 75% (range 71.6—78.4%) when alder leaves were ingested and about 30% (range 28.7—33.7%) when only larch litter was eaten. These data are very high even when compared with the 11.6—28.5% recorded for earthworms investigated by CROSSLEY *et al.* (1971), but resemble the data SHACHAK *et al.* (1976) ha~~s~~ve found. In their studies assimilation efficiency of a plant-only diet was relatively high, ranging from 50.8—81.9%, but when the diet included soil particles efficiency was reduced to 25%. Despite the lowered assimilation efficiency in *Hemilepistus reaumuri* a rise in survival resulted from the addition of soil to their diet.

We did not find any increase in mass in our feeding boxes for *Lumbricus rubellus*. But at 15 °C there could be an individual mass loss up to 20%. This could occur either by adverse conditions in the feeding chambers or by an unfavourable or unbalanced diet. We assume a plant-only diet is not optimal for *Lumbricus rubellus*.

5. Zusammenfassung

[Nahrungsaufnahme und Assimilation bei *Lumbricus rubellus* (Lumbricidae)]

Untersuchungen zur Nahrungsaufnahme und -verwertung wurden bei den Temperaturen von 5 und 15 °C durchgeführt.

Wurde *L. rubellus* HOFFMEISTER, 1843 im Mai mit Lärchennadeln gefüttert, so lag die Nahrungsaufnahme bei 3,08 ± 1,27 mg g^{-1} d^{-1} (bei 15 °C) bzw. bei 0,64 ± 0,57 mg g^{-1} d^{-1} (bei 5 °C). Von Erlenblättern, die in Parallelserien angeboten wurden, fraßen die Regenwürmer 7,59 ± 1,56 mg g^{-1} d^{-1} bzw. 2,72 ± 0,55 mg g^{-1} d^{-1}. Während der Wintermonate trat bei beiden Temperaturen eine signifikante Abnahme in der Konsumption auf.

Die Kotproduktion war von der Nahrung unabhängig und lag bei der Lärchenstreu um 2,30 mg g^{-1} d^{-1} und beim Erlenlaub um 2,35 mg g^{-1} d^{-1} (bei 15 °C). Mit Q_{10} = 3,8—5,3 erwies sich die Egestion als deutlich temperaturabhängig.

Die energetische Ausnutzung der Nahrung wird vom Nahrungsangebot, nicht aber von der Temperatur bestimmt. So konnte Erlenlaub durchschnittlich zu 75% assimiliert werden, während Lärchennadeln nur zu 30% verwertet wurden.

Bei den durchgeführten Untersuchungen konnte in den Zuchtbehältern keine Massenzunahme der Regenwürmer erzielt werden. Wir vermuten, eine Nahrung, die ausschließlich aus organischer Substanz besteht, ist auch für Oberflächenarten wie *L. rubellus* nicht günstig.

6. Acknowledgement

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Feeding experiments with *Lumbricus rubellus* were carried out at 5 and 15 °C. When *L. rubellus* was provided with larch litter in May at 15 °C consumption rate was 3.08 ± 1.27 mg g^{-1} d^{-1} and 0.64 ± 0.57 at 5 °C. Using alder leaves as a food source, consumption increased to 7.59 ± 1.56 mg g^{-1} d^{-1} and 2.72 ± 0.55 respectively. During winter months at the same temperatures decrease in consumption occurred although in the field cocoon production did not totally cease. Egestion rates were independent of food source, but were influenced by temperature ($Q_{10} = 3.8$—5.3). Assimilation efficiencies obtained from energy values were of the order of 75% for alder leaves and about 30% forl arch litter.

In the feeding experiments no increase in mass was found. An exclusively plant diet seems not to be optimal for epi-endogeic litter dwellers.

Key words: Lumbricus rubellus, consumption, egestion, assimilation, alder leaves, larch litter.